COMPARATIVE ANATOMY AND SYSTEMATIC SIGNIFICANCE OF THE INTERNAL ORGANS OF CHECKERED BEETLES. PART II. REPRODUCTIVE SYSTEMS OF THE NEW WORLD GENUS *ENOCLERUS* GAHAN (COLEOPTERA: CLERIDAE)[1]

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Abstract

Internal reproductive systems of 65 species of *Enoclerus* were studied, illustrated, described, and discussed. Outstanding interspecific variations occur only among male organs and involve accessory glands and testes. Accessory glands are referred to as medial and lateral, and their development within species may be as follows: Both glands uniramous; medial gland biramous, lateral gland uniramous; or both glands biramous. The testis comprises 12 to 79 follicles. Female organs were not notably variable among species studied (ovariole counts were not made). Species are categorized into 3 provisional groups on the basis of type of accessory-gland development, which broadly correlates with number of testicular follicles per testis and with geographic latitude. Briefly discussed are paucity of criteria for *Enoclerus* supraspecific systematics and prospects of finding such criteria among variations of the male internal reproductive organs.

Introduction

This is the second contribution from studies concerned with the anatomy and systematic value of the internal organs of world checkered beetles. The objective of the initial contributions is to establish credible generic and infrageneric characterizations. The intent of the overall project is to provide a comparative account of the higher subtaxa. This will establish a baseline of heretofore unexploited criteria to be incorporated into studies of Cleridae phylogenetics. Crowson (1972) has already demonstrated the systematic potentialities of alimentary-canal characteristics in his review of the initial paper of the series (Ekis and Gupta 1971). More recently, I analyzed reproductive-organ variations in a systematic treatment of the genus *Perilypus* (Spinola) (Ekis 1977).

Promulgations of the series may each involve one or several genera. Groups of current systematic interest will be considered first; depending, of course, on the extent to which species of a genus are represented by fluid-preserved specimens. The aim is to capture, and include in the characterizations, the major variations of a given taxon. This study involves the reproductive systems of *Enoclerus,* a genus for which there are two previous accounts of internal anatomy; Ekis and Gupta (1971) described the alimen-

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tary canal and Ekis (1976) briefly alluded to the reproductive organs. Other accounts of clerid reproductive organs (male and/or female) are those of Stein (1847), Dufour (1825), Escherich (1893), Bordas (1898, 1900), Cholodkovsky (1913), Lesne (1938), Surtees (1961), Robertson (1961), Rebordões, *et al.* (1976), and Ekis (1977, 1977a).

MATERIALS AND METHODS

This study is based on dissection of about 150 specimens arrayed among 65 species, or approximately one-third of the known taxa of the genus. Specimens were collected or received in Pampel's fluid (glacial acetic acid, 4 pts; 40% formalin, 6 pts; 95% alcohol, 15 pts; water, 30 pts), Weaver's fixative (40% formalin, 5 pts; glacial acetic acid, 2.5 pts; chloral hydrate, 20 pts; distilled water, 72.5 pts.), 10% formaldehyde, or 70% alcohol. Whenever possible I dissected 4 specimens of each species (2 males and 2 females) to determine extent of structural variation. Dissecting techniques and disposition of reproductive organs, or parts thereof, are as described elsewhere (Ekis, 1977).

Descriptions supplement illustrations, point out important differences, and pertain only to males; female reproductive organs, generally discussed in the next section, were similar among the species studies (ovariole counts were not made). To facilitate subsequent specimen-description associations a locality record is provided and the label "Internal reproductive organs studied" is pinned beneath specimens.

Illustrations were made through an ocular grid, or camera lucida, are not to the same scale, and are presented in lateral view unless noted otherwise. Only one-half of the reproductive system is drawn. For contrast, the lateral accessory gland is figured in black, the medial accessory gland in 27.5 line (20%) Zip.a.Tone, and the vas deferens and ejaculatory duct are variously stippled. Illustrated structures noted in the text are indicated by italics at first mention.

THE REPRODUCTIVE SYSTEMS

Male

The primary components of the male reproductive system are two pairs of *accessory glands, testes, vas deferens, seminal vesicle,* and *ejaculatory duct* (Fig. 2).

The tubular accessory glands lie ventral to the digestive tract, between the testes, and often project into the metathorax. They are referred to as *medial* and *lateral* according to their attachment to the ejaculatory duct. The glands are also distinguishable by the color and texture of their secretions; the medial pair containing a fulvid, frothy substance and the lateral pair a milky-white, more granular material. Except for slight differences in width, the glands are structurally homogeneous within species. Interspecifically, they vary in length, configuration, position of diverticulae, and branching characteristics. The glands may be short (Fig. 31), and loosely convoluted (Fig. 3), or exceptionally long and tightly convoluted (Fig. 27). The medial gland is usually longer and broader than the lateral gland, may be divided into a *dorsal* and *ventral branch* (Fig. 3), and is occasionally diverticulated. The lateral gland is usually about half as long as the medial gland and, when divided, consists of an *outer* and *inner branch* (Fig. 5). Commonly the lateral gland exhibits a basal *diverticulum* (Fig. 5) that is especially well developed among species exhibiting branched glands. Subdivision of male accessory glands has also been reported in Dermestidae (Tandon 1970). Because the inner lining of the basal divertículum is similar to the inner lining of the rest of the gland one may surmise that the diverticulum is also secretory. The lateral gland of *Enoclerus pilatei* (Fig. 59), *E. zebroides* (Fig. 66), and *E. pisinnus* (Fig. 68), has a second basal diverticulum (the *basal pouch)* that differs from the other by its transparent wall and apparent nonsecretory inner lining; it probably functions as a reservoir for glandular secretions. Another peculiarity of lateral-gland development is the presence of a pair of luminal ridges in *E. rosmarus, E. sericeus,* and *E. nelsoni.* These ridges appear to divide the inner lining of the gland into two secretory regions. The product of one of these is externally manifested by a dark longitudinal streak. Similar accessory gland development was found in *Colyphus cylindricus* (Gorham) (Ekis 1977a) and among species of *Perilypus* Spinola (Ekis 1977).

The testis consists of 12 to 79 tubular follicles, is oblong or subspherical, invested by a peritoneal membrane, and connects to the vas deferens via groups of 2, 3, or 4 vasa efferentia. Members of a pair of testes do not always contain equal numbers of follicles. The vas deferens is usually about half as long as the testis, but is exceptionally long in *E. fugitivus* (Fig. 20) and conspicuously robust in *E. sphegeus* (Fig. 29), *E. ichneumonius* (Fig. 3), and *E. quadrisignatus* (Fig. 26). The seminal vesicle is well developed in most species and in some appears to comprise the entire length of the vas deferens (Fig. 3). The ejaculatory duct varies in length and width, being particularly robust in *E. crabronarius* (Fig. 38) and *E. nelsoni* (Fig. 12).

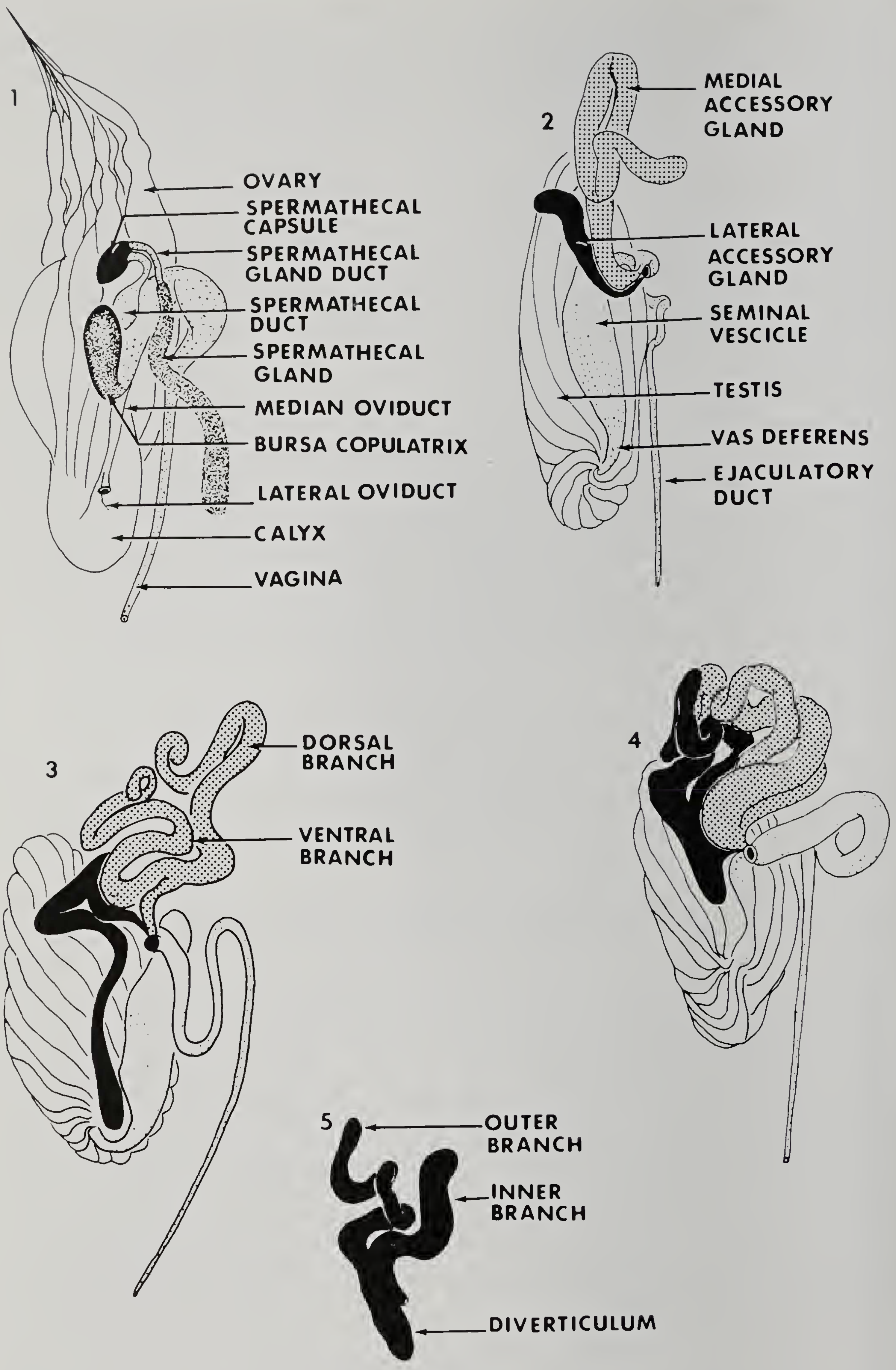
Female

The major components of the female reproductive system are the *spermathecal capsule, spermathecal gland* and its *duct, bursa copulatrix, ovaries, lateral* and *median oviducts,* and *vagina.* I consider the structural development of the female reproductive organs of *Enoclerus sphegeus* (Fig. 1) as standard for *Enoclerus.*

The spermathecal capsule lies above the vagina, between the ovaries. The capsule is an ovate, visibly sclerotized cylinder that is attached to the vagina via a basally swollen spermathecal duct. The latter opens into the vagina behind the bursa copulatrix, which essentially is an upcurved sac-like extension of the anterior vaginal area. The spermathecal gland is about 6 times longer than the spermathecal capsule with which it is linked via a short spermathecal-gland duct. The ovaries are connected anteriorly by ligaments, lie at the sides of the digestive tract, and consist of 12 or more acrotrophic ovarioles. These empty into an infolded *calyx* that contains a yellow secretion whenever mature oocytes are present. An apparently similar secretion, thought to function as an adhesive, was reported in Chrysomelidae (Gupta and Riley 1967). The lateral oviducts unite posteriorly to form the median oviduct that connects to the vagina at the base of the bursa copulatrix. The vagina, an elongate chamber, is broad at its anterior third and tapered in the remainder.

SPECIES GROUPS AND SPECIES

Species are categorized into groups in accordance with their type of accessory-gland development. This arrangement serves mainly to shorten descriptions and accentuate supraspecific differences; no definitive species-group classification is implied.



Figs. 1-5.—Internal reproductive systems. 1, female, *E. sphegeus*. 2, male, *E. beatus* (ventral). 3, male, *E. ichneumonius*. 4, male, *E. artifex*. 5, lateral accessory gland, *E. artifex*.

Group I

The species of this group have uniramous accessory glands of which the lateral is consistently shorter. The testis is usually composed of 12 follicles. Most of the species of this group occur in North America.

Enoclerus beatus (Gorham). Fig. 2
Medial gland about 4 times longer than lateral gland; testis composed of 12 follicles (2 specimens examined). Figured specimen from Mexico, Oaxaca, 19.2 km. SE El Camaron, 12.VIII.74 (C. W. O'Brien).

Enoclerus lecontei (Wolcott). Fig. 6
Glands longer than in previous species, medial gland about twice length of lateral gland; testis composed of 13-17 follicles (6 specimens examined). Figured specimen from USA, New Mexico, Timberton, 15.V.72 (C. W. O'Brien).

Enoclerus nigrifrons (Say). Fig. 7
Glands highly convoluted and with length proportion as in previous species (3 specimens examined). Figured specimen from USA, North Carolina, Research Triangle Park, 22.V. to 1.VII.69 (G. D. Hertel).

Enoclerus nigripes (Say). Fig. 8
Medial gland about 3 times longer than lateral gland; testis composed of 12 follicles (3 specimens examined). Figured specimen from USA, Missouri, Nevada, Vernon Co., 13.IV.72 (J. McReynolds).

Enoclerus ocreatus (Horn). Fig. 9
Lateral gland tightly convoluted at apical and basal third, and about half as long as medial gland; testis composed of 11-12 follicles (6 specimens examined). Figured specimen from USA, New Mexico, Timberton, 15.V.72 (C. W. O'Brien).

Enoclerus rosmarus (Say). Fig. 10
Glands robust and briefly lobate basally, medial gland slightly longer than distally coiled lateral gland, latter with luminal septum; testis composed of 11-12 follicles (4 specimens examined). Figured specimen from USA, Missouri, Columbia, 19.VI.66 (W. S. Craig).

Enoclerus schaefferi (Barr). Fig. 11
Medial gland about 3 times longer than lateral gland; testis composed of 13 follicles (1 specimen examined). Figured specimen from USA, Oregon, Curry Co., VI.72 (G. Steyskal).

Enoclerus nelsoni Barr. Fig. 12
Glands robust, medial gland only slightly longer than coiled lateral gland, latter lobate basally and with luminal septum; testis composed of 12 follicles (1 specimen examined). Figured specimen from Mexico, Oaxaca, 43 km. W Jalapa del Marquez, 22.IV.73 (G. Hevel).

Enoclerus aethiops Barr. Fig. 13
Medial gland about twice length of lateral gland; testis composed of 12 follicles (2 specimens examined). Figured specimen from Mexico, Chiapas, San Christobal de las Casas, 5.VI.74 (C. W. O'Brien).

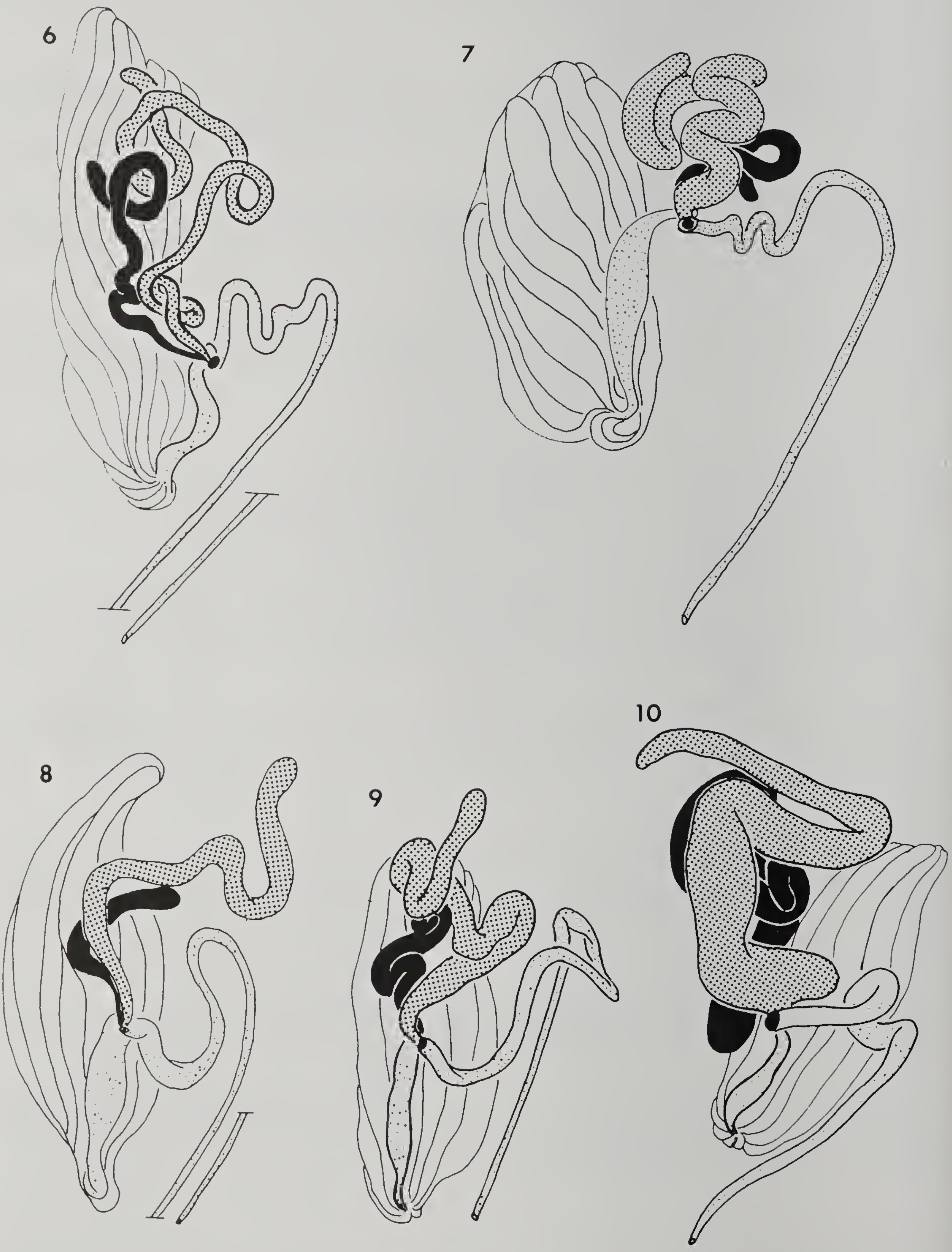
Enoclerus albosignatus Ekis, *E. auripilus* Ekis, *E. sericeus* Ekis, and *E. vulnus* Ekis also belong to Group I. The internal reproductive organs of these species were described and figured elsewhere (Ekis 1976).

Group II

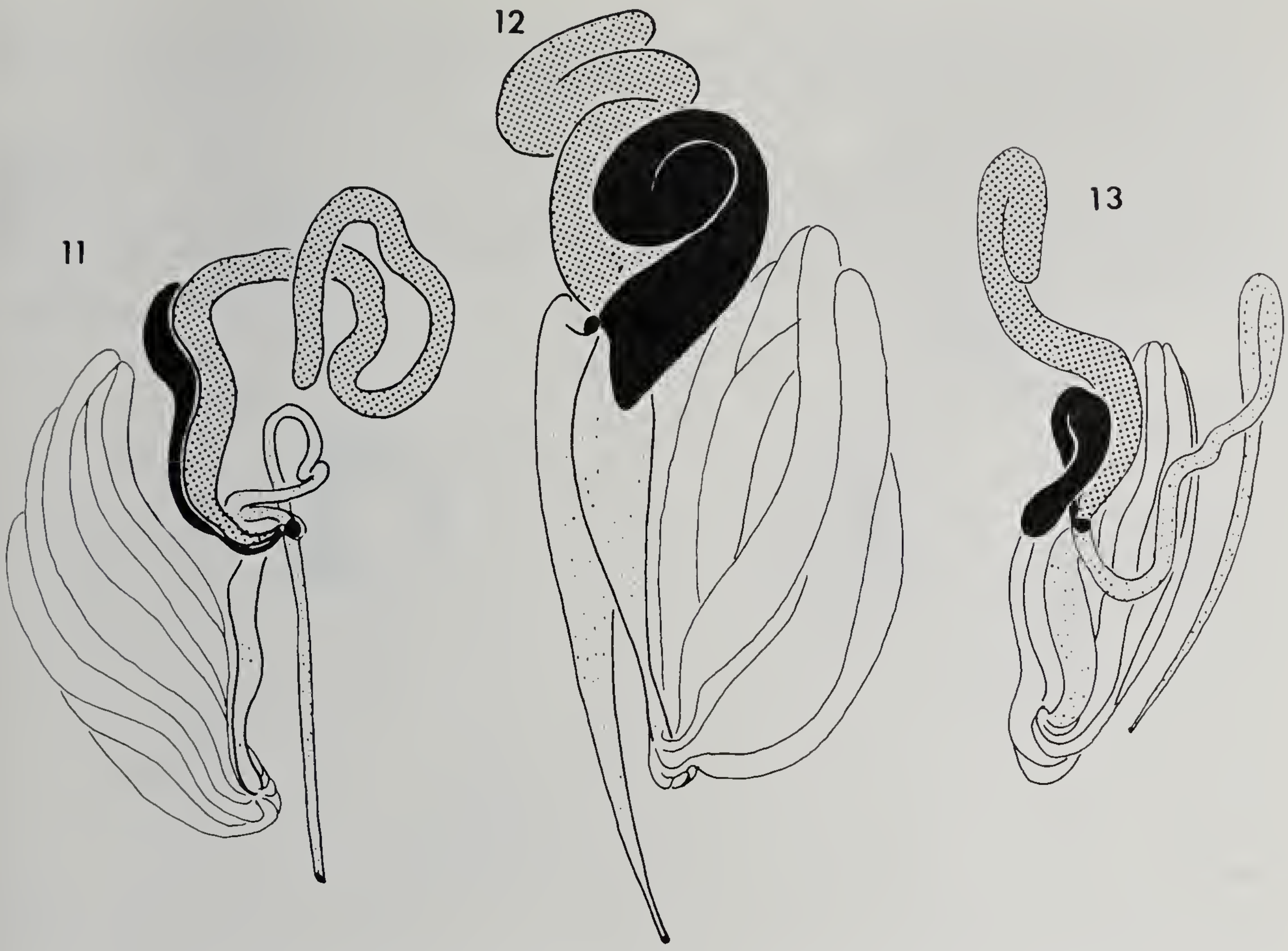
In this group the medial accessory gland is biramous and usually much longer than the uniramous lateral gland; of the two medial-gland branches the ventral is longer. The testis is usually composed of more than

24 follicles. Most of the species of this group occur in southern North America and/or Central America.

Enoclerus barri Knull. Fig. 14
Ventral branch of medial gland diverticulated distally; testis composed of 30 follicles (2 specimens examined). Figured specimen from USA, California, Yosemite National Park, summer 1970.



Figs. 6-10.—Male internal reproductive systems. 6, *E. lecontei*. 7, *E. nigrifrons*. 8, *E. nigripes*. 9, *E. ocreatus*. 10, *E. rosmarus*.



Figs. 11-13.—Male internal reproductive systems. 11, *E. schaefferi* (ventral). 12, *E. nelsoni* (ventral). 13, *E. aethiops*.

Enoclerus coccineus (Schenkling). Fig. 15
Glands longer than in previous species; testis composed of 12 follicles (2 specimens examined). Figured specimen from USA, New Mexico, 32 km. NW Melrose, 22.VI.61 (J. H. Russell).

Enoclerus cordifer (Le Conte). Fig. 16
Dorsal branch of medial gland tightly convoluted distally and much longer than broadly curvate lateral gland (1 specimen examined). Figured specimen from USA, Colorado, Nunn, 3.VIII.71 (R. J. Lavigne).

Enoclerus decussatus (Klug). Fig. 17
Glands swollen basally, tapered distally; lateral gland about half length of either branch of medial gland; testis composed of 39 follicles (2 specimens examined). Figured specimen from Mexico, Durango, 24 km. W Durango, 18.VIII.74 (C. W. O'Brien).

Enoclerus dichrous Chapin. Fig. 18
Lateral gland with two diverticulae at basal half (1 specimen examined). Figured specimen from Bolivia, Tumupasa, XII.1921-1922 (W. M. Mann).

Enoclerus eximius (Mannerheim). Fig. 19
Lateral gland recurved medially; testis composed of 25-30 follicles (3 specimens examined). Figured specimen from USA, California, Alameda Co., V.72 (W. H. Tyson).

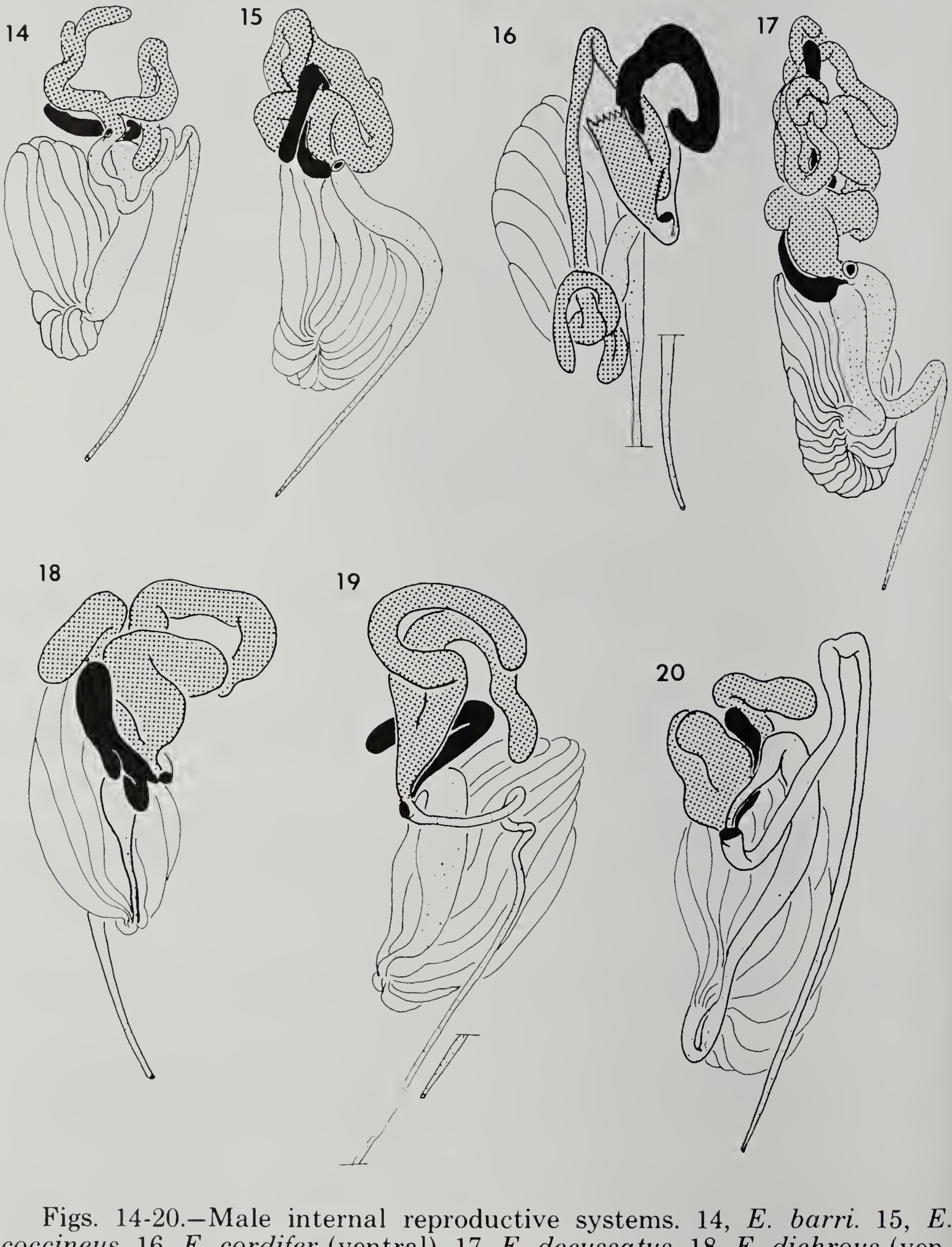
Enoclerus fugitivus var. *cupidus* Wolcott. Fig. 20
Lateral gland much narrower than medial gland, latter with very short dorsal branch; vas deferens conspicuously long; testis composed of 24 follicles (3 specimens examined). Figured specimen from Costa Rica, Cartago, Turrialba, 4.VI.73 (G. Ekis).

Enoclerus hogei (Gorham). Fig. 21

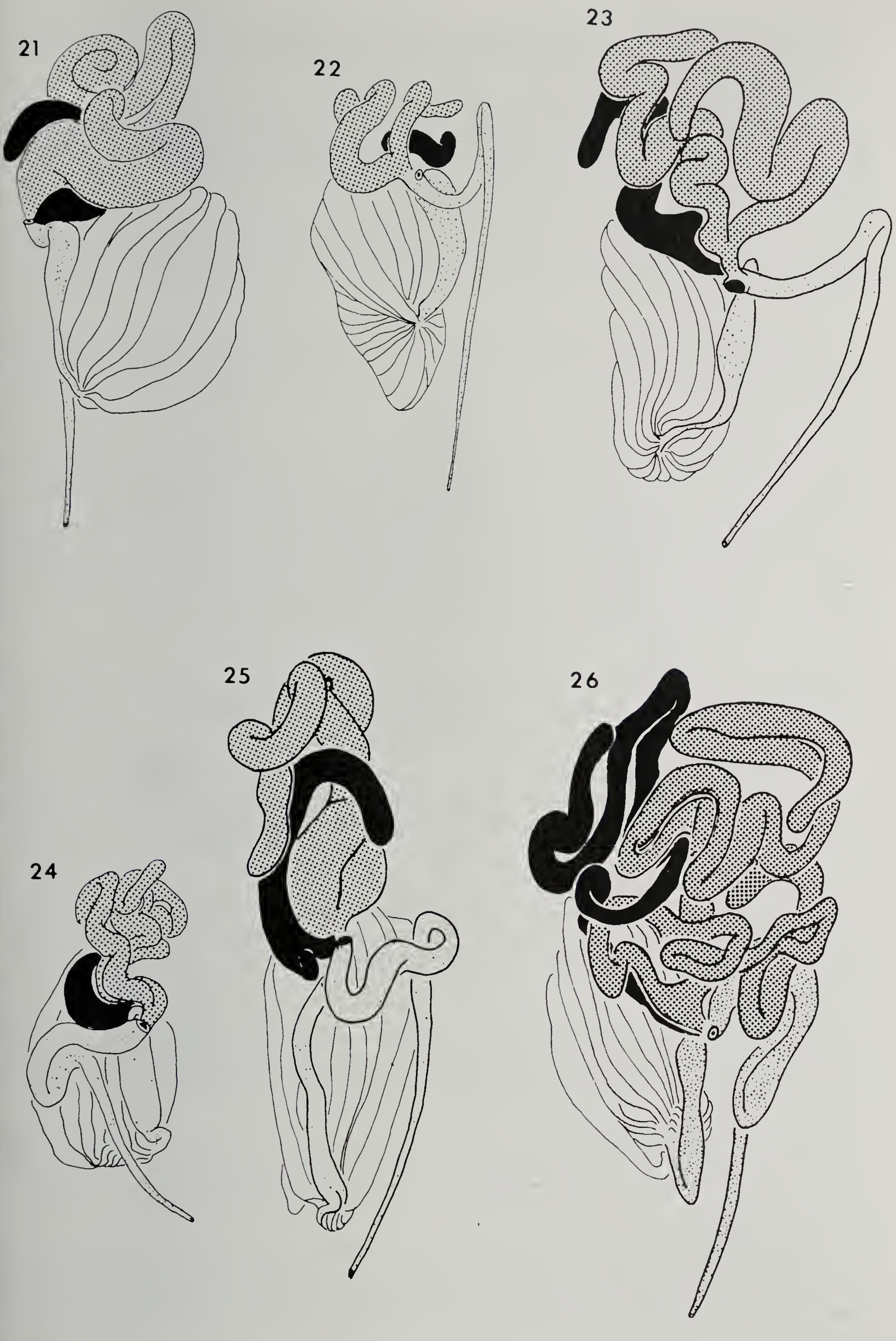
Lateral gland broadly arcuate; testis spheroid, composed of 40 follicles (1 specimen examined). Figured specimen from Mexico, Chiapas, 3.2 km. E Rizo de Oro, 1.VIII.74 (C. W. O'Brien).

Enoclerus ichneumonius (Fabricius). Fig. 3

Lateral gland about same length as branches of medial gland; testis composed of more than 30 follicles (1 specimen examined). Figured specimen from USA, Florida, Jefferson Co., 25.V.69 (W. H. Whitcomb).



Figs. 14-20.—Male internal reproductive systems. 14, *E. barri*. 15, *E. coccineus*. 16, *E. cordifer* (ventral). 17, *E. decussatus*. 18, *E. dichrous* (ventral). 19, *E. eximius*. 20, *E. fugitivus* var. *cupidus*.



Figs. 21-26.—Male internal reproductive systems. 21, *E. hogei* (ventral). 22, *E. lugubris*. 23, *E. lunatus*. 24, *E. opifex*. 25, *E. quadrinodosus*. 26, *E. quadrisignatus*.

Enoclerus lugubris (Erichson). Fig. 22
Glands conspicuously short; testis composed of 24 follicles (2 specimens examined). Figured specimen from Brazil, Mato Grosso, Sinop, X.74 (M. Alvarenga).

Enoclerus lunatus (Klug). Fig. 23
Lateral gland long, with diverticulum near base; testis composed of 12-13 follicles (1 specimen examined). Figured specimen from USA, Florida, Gainesville, 27.VI.69 (R. E. Woodruff).

Enoclerus opifex (Gorham). Fig. 24
Lateral gland about equal in length to dorsal branch of medial gland; testis composed of 12 follicles (3 specimens examined). Figured specimen from Mexico, Sinaloa, Mazatlan, VIII.73 (J. Chemsak).

Enoclerus quadrinodosus (Chevrolat). Fig. 25
Lateral gland broadly arcuate and diverticulated basally; testis composed of about 29 follicles (1 specimen examined). Figured specimen from Mexico, Chiapas, Hwy. 91, 23.VI.73 (G. Ekis).

Enoclerus quadrisignatus (Say). Figs. 26-28
Glands extremely long; lateral gland about equal in length to branches of medial gland; testis composed of 42-52 follicles (5 specimens examined). Figured specimen from USA, Arizona, Nogales, 8.IX.69 (P. Laddy and R. A. Nicholson).

Remarks: Specimens of this species from Southern Mexico differ from their northern counterparts as follows; lateral gland one-third length of branches of medial gland, latter set on long stalk, and testis composed of more than 61 follicles (1 specimen examined). Figured specimen (Figs. 27, 28) from Mexico, Oaxaca, 68.6 km. W Jalapa del Marquez, 22.IV.73 (G. Hevel).

Enoclerus sphegeus (Fabricius). Fig. 29
Lateral gland longer than dorsal branch of medial gland; testis composed of 12 follicles (2 specimens examined). Figured specimen from Guatemala, Suchitepequez, Zapotitlan, Finca Las Nubes, 16.VI.73 (G. Ekis).

Enoclerus versicolor (Laporte). Fig. 31
Glands robust and short, lateral gland sinuatotruncate distally; testis composed of 24 follicles (2 specimens examined). Figured specimen from Panama, Cerro Campana, 31.XII.73 (H. P. Stockwell).

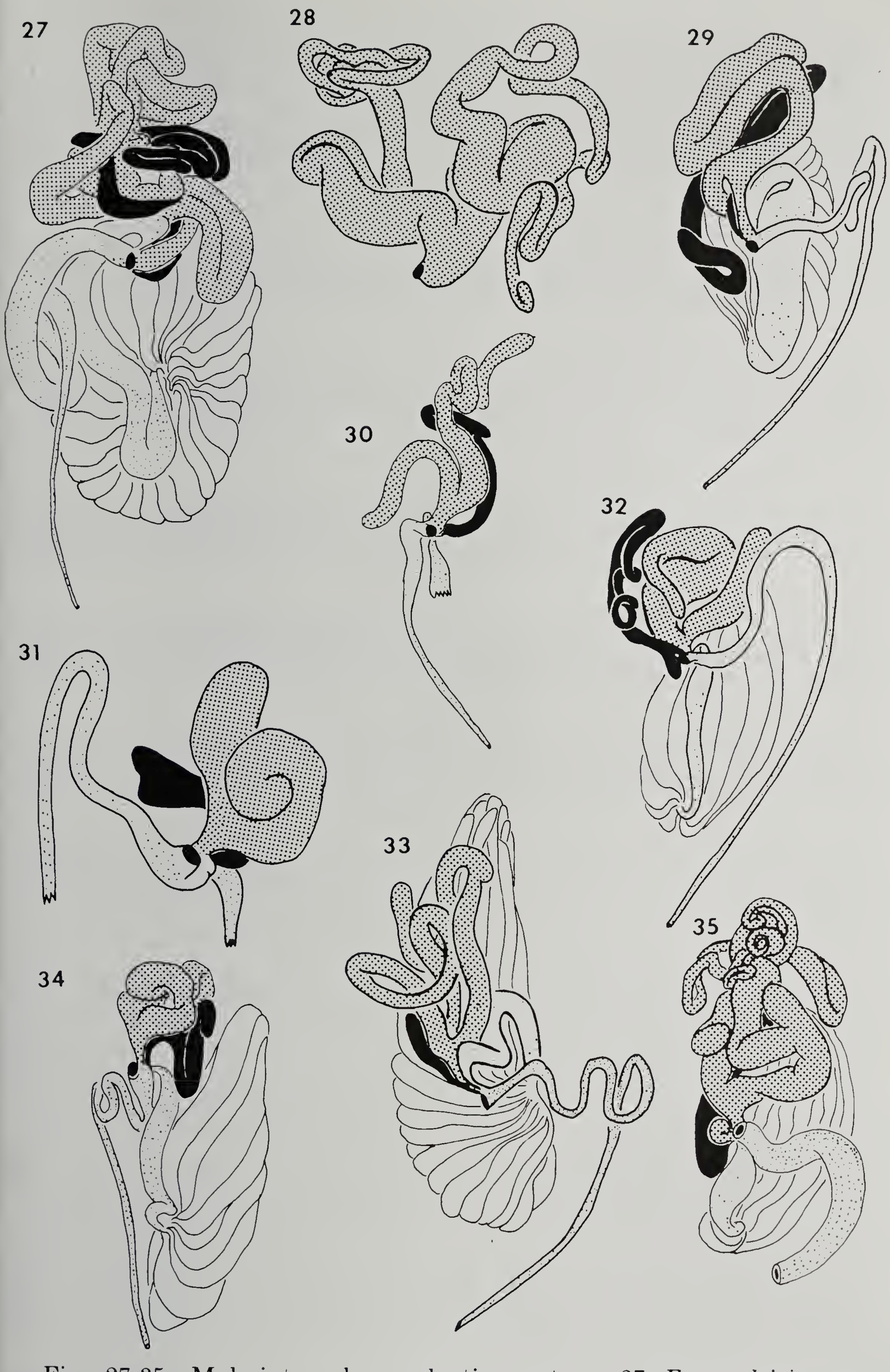
Enoclerus villicus (Gorham). Fig. 32
Lateral gland conspicuously narrow, coiled distally, diverticulated basally, and one-third longer than ventral branch of medial gland; testis composed of 17 follicles (4 specimens examined). Figured specimen from Costa Rica, Cartago, Turrialba, 12.VII.71 (G. Ekis).

Enoclerus zonatus (Klug). Fig. 33
Lateral gland notably short; dorsal branch of medial gland diverticulated at middle; testis composed of 68-79 follicles (3 specimens examined). Figured specimen from USA, Texas, 20.8 km. W Del Rio, Val Verde Co., 9.V.71 (D. E. Foster).

Enoclerus irregularis Barr. Fig. 34
Glands short; testis composed of 34 follicles (1 specimen examined). Figured specimen from Honduras, Comayagua, 9 km. NW Siquatepeque, 19.VII.74 (C. O'Brien).

Enoclerus signifer Barr. Fig. 35
Lateral gland convoluted and very narrow distally, much longer than branches of medial gland, latter diverticulated basally; dorsal branch of medial gland with lobate diverticulum; testis composed of 24 follicles (1 specimen examined). Figured specimen from Panama, Canal Zone, Barro Colorado Island, 4-11.VII.41 (Collector unknown).

The internal reproductive organs of *Enoclerus erwini* Ekis, *E. gibbus* Ekis, and *E. whiteheadi* Ekis which also belong to this group were described elsewhere (Ekis 1976).



Figs. 27-35.—Male internal reproductive systems. 27, *E. quadrisignatus*. 28, same, medial accessory gland. 29, *E. sphegeus*. 30, *E. tubercularis*. 31, *E. versicolor*. 32, *E. villicus*. 33, *E. zonatus*. 34, *E. irregularis*. 35, *E. signifer*.

Group III

The members of Group III have biramous accessory glands (but see *E. dimidiatus).* The lateral gland is diverticulated basally and has the outer branch consistently longer and more slender than the inner branch. The testis usually consists of 12 follicles. Most of the species of this group occur in South America.

Enoclerus artifex (Spinola). Figs. 4, 5
Branches of lateral gland set on long stalk, outer branch about twice length of inner branch; testis composed of 37 follicles (2 specimens examined). Figured specimen from Brazil, Mato Grosso, Sinop, X.74 (M. Alvarenga).

Enoclerus bilobus (Spinola). Figs. 36, 37
Outer branch of lateral gland about 3 times longer than inner branch and only slightly shorter than branches of medial gland; testis composed of 12 follicles (2 specimens examined). Figured specimen from Brazil, Sao Paulo, San Jose Barreiro, XI.70 (M. Alvarenga).

Enoclerus crabronarius (Spinola). Figs. 38, 39
Medial gland exceptionally long, tapered distally, outer branch of lateral gland diverticulated medially; testis composed of more than 41 follicles (1 specimen examined). Figured specimen from Costa Rica, Cartago, Turrialba, 5.VI.73 (G. Ekis).

Enoclerus comptus (Klug). Fig. 40
Ventral branch of medial gland about twice length of dorsal branch; testis composed of 12 follicles (2 specimens examined). Figured specimen from Brazil, Santa Catarina, Nova Teutonia, XI.74 (F. Plaumann).

Enoclerus dimidiatus (Schenkling). Figs. 41, 42
Lateral gland trilobed, inner branch bifurcated; testis composed of 24 follicles (1 specimen examined). Figured specimen from Mexico, 14.4 km. SE Izucar de Metamoros, 1.VI.74 (C. W. O'Brien).

Enoclerus distinctus (Spinola). Figs. 43, 44
Outer branch of lateral gland about twice length of inner branch; testis composed of 12 follicles (2 specimens examined). Figured specimen from locality as noted for *E. bilobus.*

Enoclerus fasciicollis (Schenkling). Figs. 45, 46
Outer branch of lateral gland exceptionally long, about 4 times longer than inner branch; testis composed of 12 follicles (4 specimens examined). Figured specimen from locality as noted for *E. comptus.*

Enoclerus imperialis (Spinola). Figs. 49, 50
Inner branch of lateral gland one-third shorter than outer branch; testis composed of 12 follicles (1 specimen examined). Figured specimen from Brazil, Mato Grosso, X.73 (M. Alvarenga).

Enoclerus laetus (Klug). Fig. 51
Lateral gland branches recurved medially; testis composed of 11-13 follicles (4 specimens examined). Figured specimen from Mexico, Nuevo Leon, 4.8 km. W Linares, 22.IX.75 (J. Chemsak).

Enoclerus laportei (Spinola).
Glands and testis as in *E. imperialis* (2 specimens examined). Figured specimen from locality as noted under *E. comptus.*

Enoclerus meridanus (Chevrolat). Figs. 52, 53
Outer branch of lateral gland 3 times longer than inner branch; testis composed of 12 follicles (2 specimens examined). Figured specimen from Panama, Cerro Campana, 29.VI.74 (C. W. O'Brien).

Enoclerus militaris (Schenkling). Fig. 54
Outer branch of lateral gland only slightly longer than inner branch (1 specimen examined). Figured specimen from Brazil, Sao Paulo, San Jose Barreiro, XI.70 (M. Alvarenga).

Enoclerus miniatus (Spinola). Fig. 55
Outer branch of lateral gland only slightly longer than inner branch; testis composed of 12 follicles (2 specimens examined). Figured specimen from Brazil, Rio de Janeiro, Guanabara, II.72 (M. Alvarenga).

Enoclerus nigromaulatus (Chevrolat). Figs. 56-58
Dorsal branch of medial gland diverticulated medially; testis composed of 13 follicles (1 specimen studied). Figured specimen from Mexico, Tabasco, La Chontalpa, 29.IV.73 (G. Ekis).

Enoclerus pilatei (Chevrolat). Fig. 59
Inner branch of lateral gland with basal pouch and only slightly shorter than outer branch; testis composed of 12 follicles (2 specimens examined). Figured specimen from Mexico, Tabasco, La Chontalpa, 4.VIII.71 (G. Ekis).

Enoclerus planonotatus (Laporte). Fig. 60
Outer branch of lateral gland convoluted distally; testis composed of 12 follicles (2 specimen examined). Figured specimen from locality as noted under *E. comptus.*

Enoclerus salvini (Gorham). Fig. 61
Outer branch of lateral gland 3 times longer than recurved inner branch; testis composed of 13 follicles (2 specimens examined). Figured specimen from Guatemala, Antigua, 20.VI.73 (G. Ekis).

Enoclerus xalbum (Gorham). Fig. 62
Lateral-gland diverticulum broadened, inner branch of lateral gland recurved medially; testis composed of 12 follicles (2 specimens examined). Figured specimen from Costa Rica, Alajuela, VI.69 (G. Ekis).

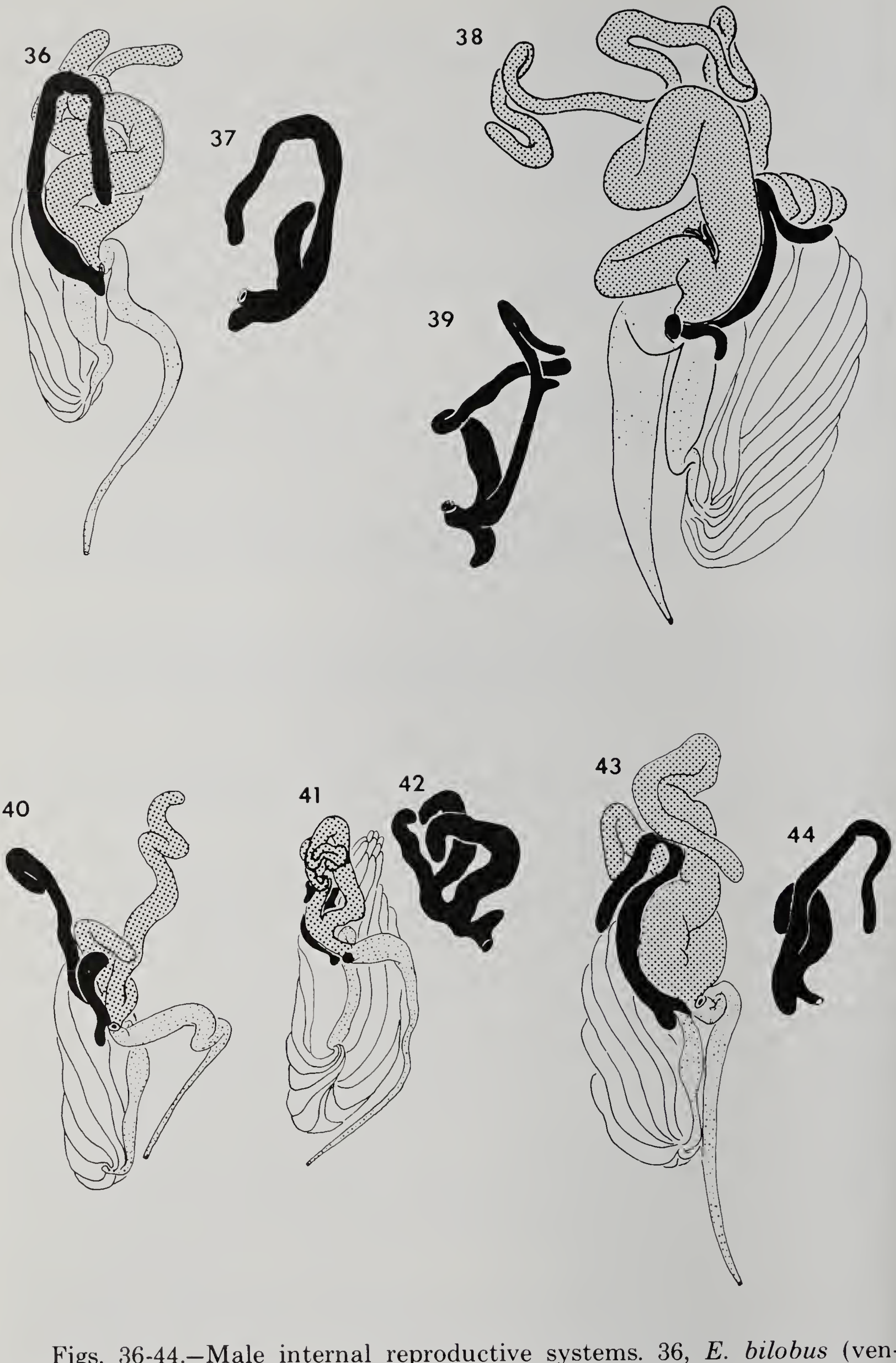
Enoclerus zebra (Chevrolat). Figs. 63, 64
Outer branch of lateral gland slightly longer than inner branch; testis composed of 17 follicles (1 specimen examined). Figured specimen from El Salvador, 44.8 km. W Libertad, 8.VI.74 (C. W. O'Brien).

Enoclerus zebroides Barr. Figs. 65, 66
Lateral gland with basal pouch; testis composed of 12 follicles (1 specimen examined). Figured specimen from Panama, Canal Zone, Pipe Line Road, 30.VI.74 (C. W. O'Brien).

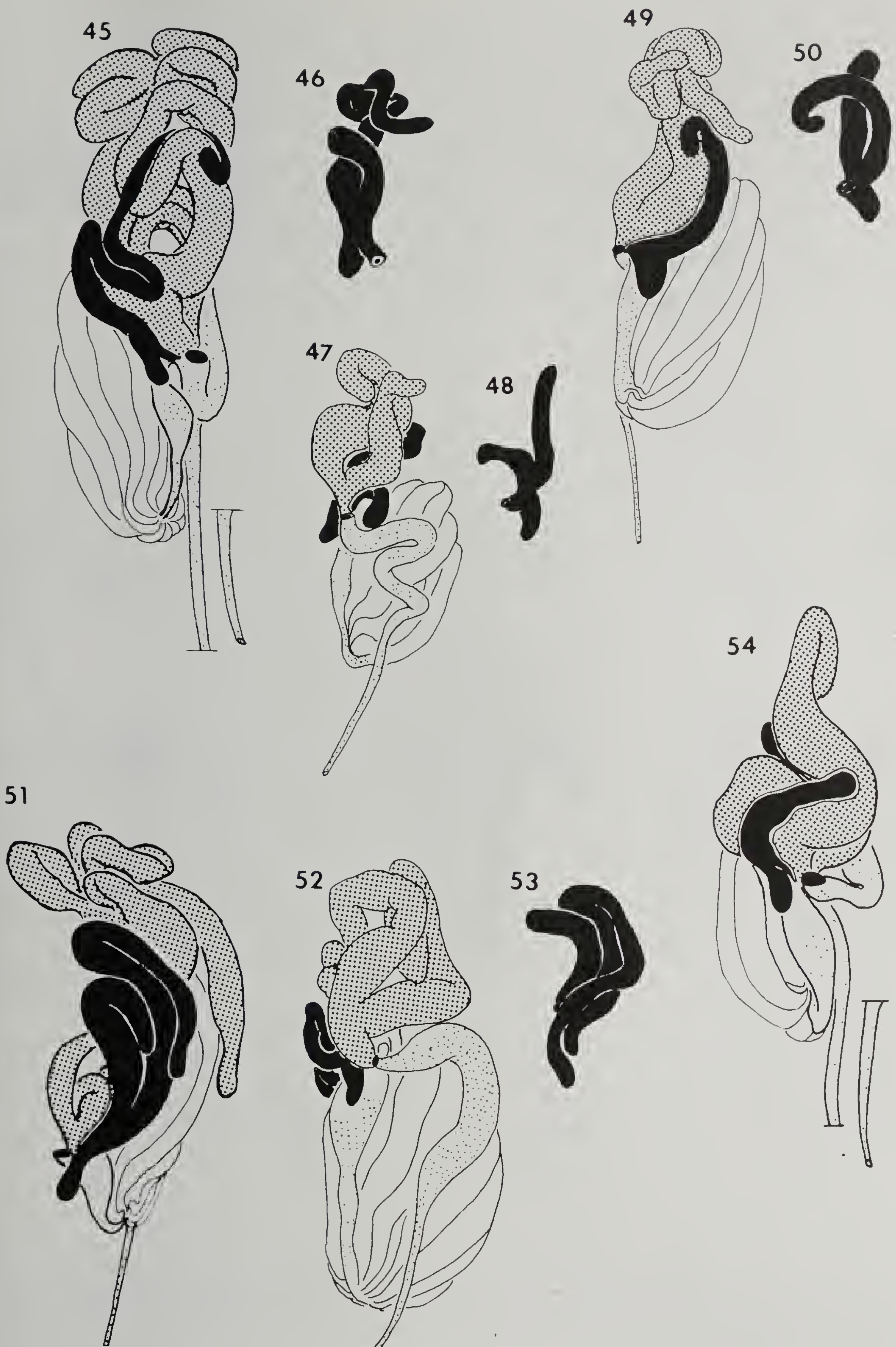
Enoclerus tricinctus (Chevrolat) Fig. 67
Outer branch of lateral gland only slightly longer than inner branch; testis composed of 12 follicles (1 specimen examined). Figured specimen from Brazil, Mato Grosso, Villa Vera, X.13, (M. Alvarenga).

Enoclerus pisinnus Barr Fig. 68
Outer branch of lateral gland about twice length of inner branch; testis composed of 12 follicles (1 specimen examined). Figured specimen from Venezuela, Aragua, Rancho Grande, 14.VIII.73 (J. Clavijo).

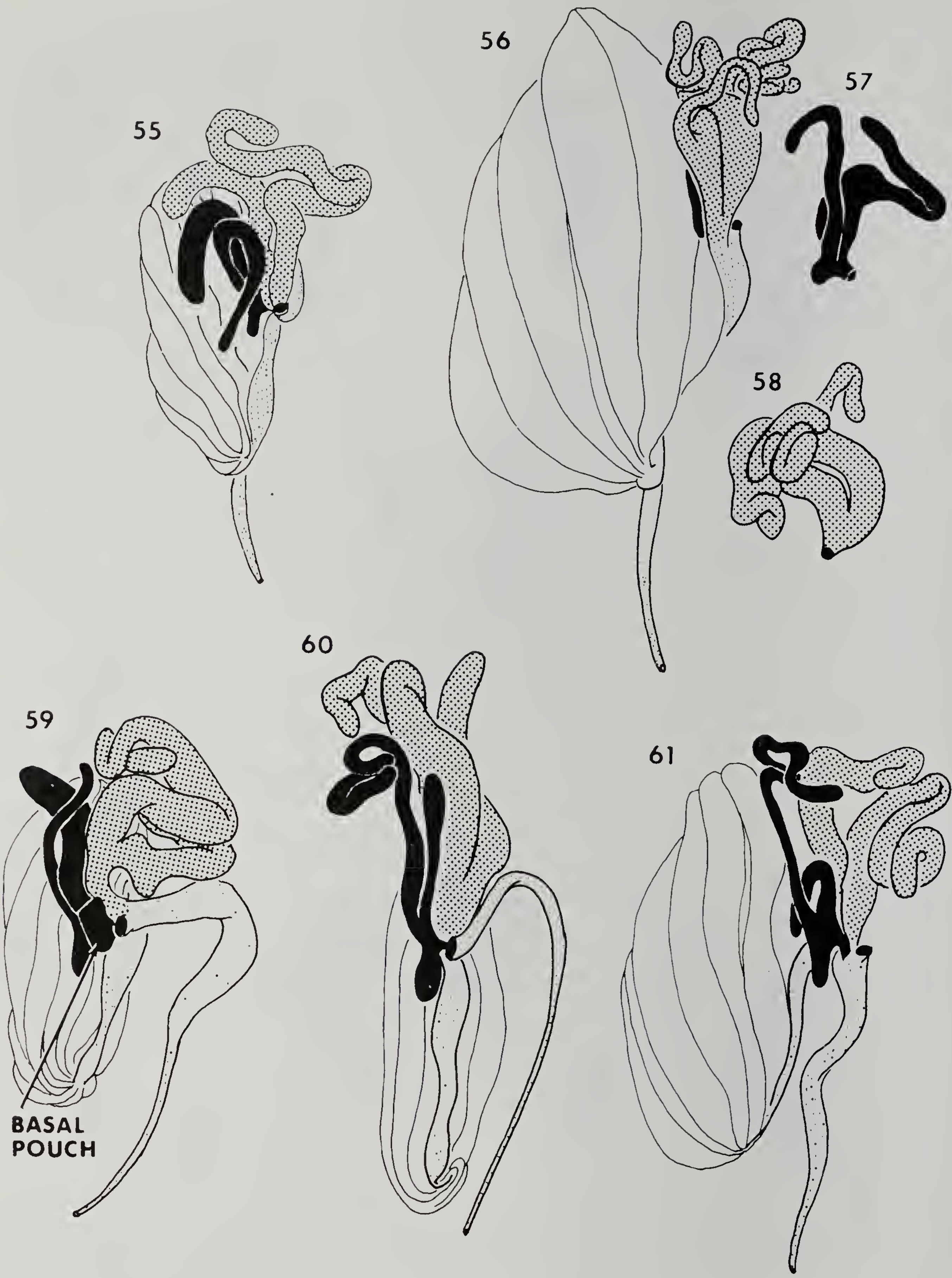
Enoclerus alvarengai Ekis, *E. canus* Ekis, *E. obrieni* Ekis, *E. sagittarius* Ekis, and *E. leehermani* Ekis also belong to this group. The internal reproductive organs of these species were described by Ekis (1976).



Figs. 36-44.—Male internal reproductive systems. 36, *E. bilobus* (ventral). 37, same, lateral accessory gland. 38, *E. crabronarius* (ventral). 39, same, lateral accessory gland. 40, *E. comptus*. 41, *E. dimidiatus*. 42, same. lateral accessory gland. 43, *E. distinctus* (ventral). 44, same, lateral accessory gland.



Figs. 45-54.—Male internal reproductive systems. 45, *E. fasciicollis* (ventral). 46, same, lateral accessory gland. 47, *E. flavosignatus*. 48, same, lateral accessory gland. 49, *E. imperialis* (ventral). 50, same, lateral accessory gland. 51, *E. laetus* (ventral). 52, *E. meridanus*. 53, same, lateral accessory gland. 54, *E. militaris* (ventral).

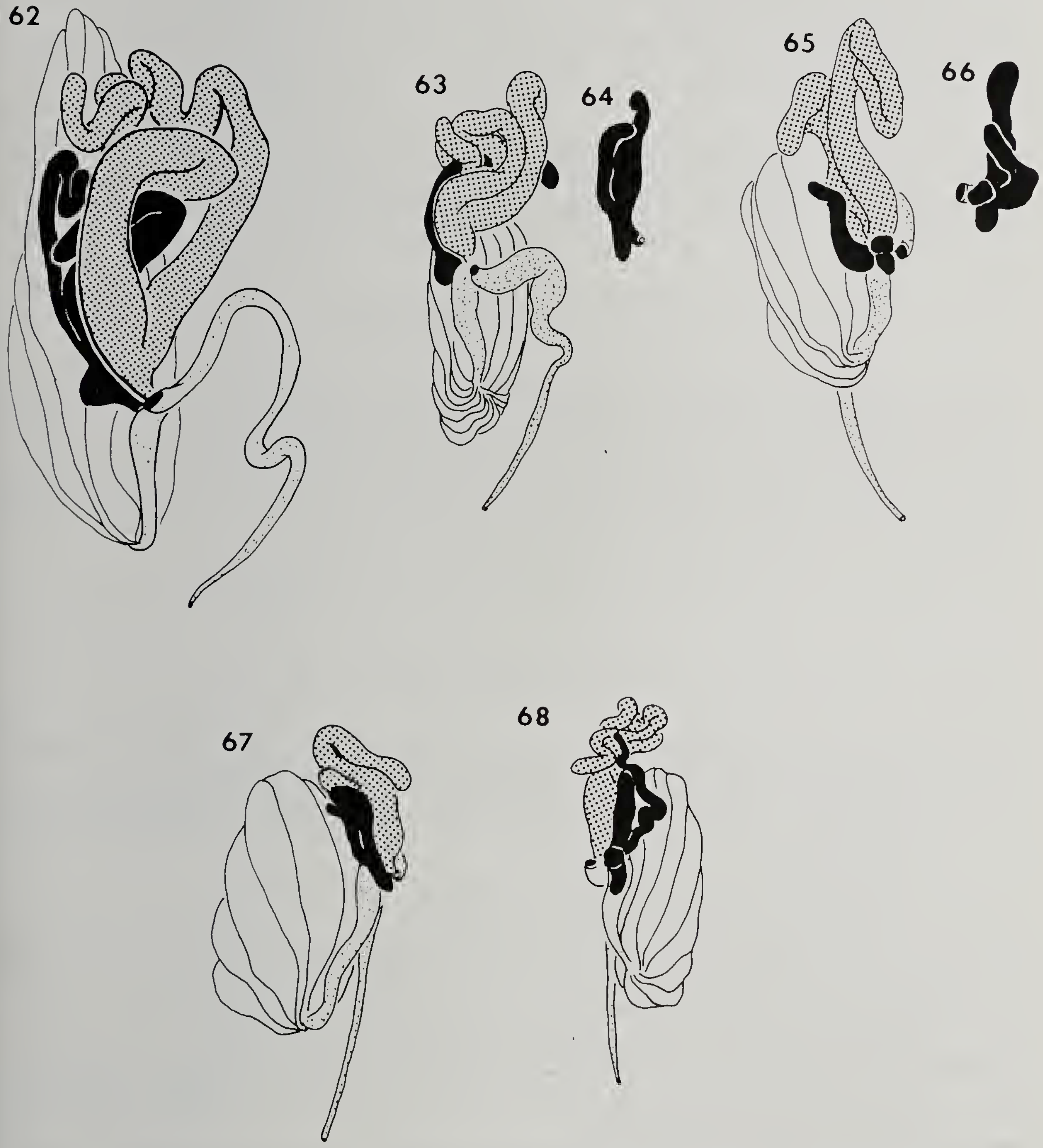


Figs. 55-61.—Male internal reproductive systems. 55, *E. miniatus* (ventral). 56, *E. nigromaculatus* (ventral). 57, same, lateral accessory gland. 58, same, medial accessory gland. 59, *E. pilatei*. 60, *E. planonotatus*. 61, *E. salvini* (ventral).

Discussion

Enoclerus (sensu Corporaal 1950) constitutes a diverse and complex assemblage of species among which adult external anatomy is apparently of minimal phylogenetic value above species level. Integumental differences are mostly species specific and thus unsuitable for predicting sister group relationships (Hennig 1966). Diagnostic characteristics involving deviate body size, shape, or color, which provide some basis for species recognition and species grouping, are of the sort that are commonly poor indicators of descent. The occurrence of such characteristics among many species of *Enoclerus* is probably more a manifestation of rigorous selection towards mimetic life styles that of common ancestry.

The above mentioned views and those expressed elsewhere (Ekis 1975, 1976) make clear that although most *Enoclerus* species are readily diagnosed by convenient anatomical characteristics, such characteristics will



Figs. 62-68.—Male internal reproductive systems. 62, *E. xalbum*. 63, *E. zebra*. 64, same, lateral accessory gland. 65, *E. zebroides* (ventral). 66, same, lateral accessory gland. 67, *E. tricinctus* (ventral). 68, *E. pisinnus* (ventral).

not alone generate adequate information for discussions of interspecific relationships. Therefore, the advancement of *Enoclerus* systematics beyond descriptive stages will require study of more than conventional suites of anatomical characteristics. Certainly the field work of Foster (1971), involving biology, and the larval work of Böving and Champlain (1920) forecast potentialities of heretofore unapplied systematic data. Unfortunately, available information of *Enoclerus* biology and larval anatomy is too fragmentary at present for application in theoretical systematics. In the meantime, contributions to the systematic progress of these beetles may be directed at unexploited anatomical attributes, among which may be included the internal reproductive organs.

Among *Enoclerus* males, there is substantial interspecific variation of accessory-gland development. Such variations provide a patent, supportive basis for establishment of species groups, and are a potentially rich source of information for phylogenetic studies at the suprageneric level. I emphasize, however, that herein I deal with only about one-third of the known species. Moreover, because *Enoclerus* is inadequately defined at present (Barr 1976), a discussion of the extent to which species groups I, II, and III reflect kinships must await a more holistic systematic analysis of *Enoclerus* and its allies.

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